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Respiration of aged soil carbon during fall in permafrost peatlands enhanced by active layer deepening following wildfire but limited following thermokarst

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Abstract

Permafrost peatlands store globally significant amounts of soil organic carbon (SOC) that may be vulnerable to climate change. Permafrost thaw exposes deeper, older SOC to microbial activity, but SOC vulnerability to mineralization and release as carbon dioxide is likely influenced by the soil environmental conditions that follow thaw. Permafrost thaw in peat plateaus, the dominant type of permafrost peatlands in North America, occurs both through deepening of the active layer and through thermokarst. Active layer deepening exposes aged SOC to predominately oxic conditions, while thermokarst is associated with complete permafrost thaw which leads to ground subsidence, inundation and soil anoxic conditions. Thermokarst often follows active layer deepening, and wildfire is an important trigger of this sequence. We compared the mineralization rate of aged SOC at an intact peat plateau (~70 cm oxic active layer), a burned peat plateau (~120 cm oxic active layer), and a thermokarst bog (~550 cm anoxic peat profile) by measuring respired ^{14}C–CO_2. Measurements were done in fall when surface temperatures were near-freezing while deeper soil temperatures were still close to their seasonal maxima. Aged SOC (1600 yrs BP) contributed 22.1 ± 11.3% and 3.5 ± 3.1% to soil respiration in the burned and intact peat plateau, respectively, indicating a fivefold higher rate of aged SOC mineralization in the burned than intact peat plateau (0.15 ± 0.07 versus 0.03 ± 0.03 g CO_2–C m^{-2} d^{-1}). None or minimal contribution of aged SOC to soil respiration was detected within the thermokarst bog, regardless of whether thaw had occurred decades or centuries ago. While more data from other sites and seasons are required, our study provides strong evidence of substantially increased respiration of aged SOC from burned peat plateaus with deepened active layer, while also suggesting inhibition of aged SOC respiration under anoxic conditions in thermokarst bogs.

1. Introduction

Northern permafrost peatlands are global hot spots for soil organic carbon (C) storage, with up to 250 kg C m^{-2} and an estimated total storage of 150 Pg within the northern circumpolar permafrost region (Hugelius *et al* 2014). The discontinuous permafrost zone of western Canada is a major peatland region with >150 000 km^2 of permafrost peatlands (Hugelius *et al* 2014). Peatland development in this region started about 9000 years ago, but permafrost only started aggrading after the Holocene thermal maximum and became widespread following a climate cooling around 1200 years ago (Zoltai 1995, Pelletier *et al* 2017). Peat plateaus are the dominant permafrost peatland type in this region, with 2–6 m thick peat deposits and a surface that is elevated 1–2 m above the surroundings due to excess ground ice (Zoltai 1972, Zoltai and Tarnocai 1975, Vitt *et al* 1994, Robinson and Moore 2000, Quinton *et al* 2009). Northern regions are rapidly warming (Johannessen *et al* 2004) and permafrost thaw (Payette *et al* 2004, Romanovsky *et al* 2010, Baltzer *et al* 2014) will expose vast stores of permafrost peatland C to microbial activity, and thus to potential mineralization and emission into the atmosphere as greenhouse gases carbon dioxide (CO_2) and methane (CH_4). Deep permafrost C reservoirs accumulated over millennia are depleted in radiocarbon, ^{14}C, and their release to the atmosphere represents a net C addition to the modern C cycle. The magnitude and timing of greenhouse gas emissions derived from recently thawed soil C represents a critical uncertainty for our understanding of the permafrost C feedback to climate change (Schuur *et al* 2015).

The vulnerability of aged soil C to microbial mineralization in peatland plateaus is likely influenced by the degree to which thaw causes drainage or flooding of the peat profile, thus determining the relative dominance of oxic versus anoxic conditions. In peat plateaus, the active layer is largely oxic as the elevated peat surface allows for efficient lateral drainage (Wright *et al* 2009). While active layer deepening is thus likely to expose previously frozen soil C to aerobic decomposition, mineralization rates of aged soil C may still be limited by the low soil temperatures near the base of the active layer, and by the fact that only a fraction of the peat profile has thawed. Complete permafrost thaw, however, causes substantial ground subsidence and the formation of thermokarst bogs where almost the entire peat profile becomes inundated and anoxic (Camill 1999, Turetsky *et al* 2007). While anoxic conditions may restrict respiration of aged C (Schädel *et al* 2016), studies of carbon stocks along Alaskan thermokarst bog chronosequences suggest large C losses (>30% of initial C stocks) within decades following thaw (Jones *et al* 2017). Mechanisms for such rapid C loss are currently unknown and direct field observations of aged soil C loss during or following thermokarst bog expansion have found limited contribution of aged soil C to CH_4 or CO_2 release (Klapstein *et al* 2014, Cooper *et al* 2017, Estop-Aragonés *et al* 2018). However, these studies were carried out during the growing season and in thermokarst peatlands with relatively shallow peat deposits (<2 m) while the potential for detecting aged soil C losses may be greater in fall or in larger peat deposits.

Wildfire is a dominant and increasingly common disturbance in western Canada (Gillett *et al* 2004, Kasischke *et al* 2010, Rogers *et al* 2015). Wildfire in boreal forests accelerates permafrost thaw through active layer deepening (Burn 1998, Yoshikawa *et al* 2002, Viereck *et al* 2008, Fisher *et al* 2016) and a similar response has been recently documented in burned peat plateaus, where a deeper active layer can, if permafrost is able to recover, last about 20 years (Gibson *et al* 2018). However, observations of charcoal in peat profiles (Zoltai 1993, Myers-Smith *et al* 2007) suggest that wildfire may also trigger thermokarst bog formation. Thus, both active layer deepening and thermokarst bog expansion are accelerated following wildfire and the contrasting soil environmental conditions associated with the mode of thaw may influence vulnerability of aged soil C.

We present a case study measuring the ^{14}C content of CO_2 respired from soils at the end of the growing season to assess whether and to what extent contrasting soil environmental conditions in peat plateaus and thermokarst bogs may influence the mineralization and atmospheric release of aged soil C in permafrost peatlands in northern Alberta. We selected an intact peat plateau, a burned peat plateau with a deepened active layer, and a thermokarst bog with a deep (>5 m) peat profile where distance to the peat plateau edge was related to time since thaw from decades to centuries. Sampling was done in fall when we assumed aged soil C mineralization to be near its seasonal maximum rate and thus the aged soil C contribution to total soil respiration sufficient for detection. We hypothesized higher respiration rates of aged soil C in both the burned and thermokarst sites relative to the intact peat plateau, given the larger quantity of aged soil C available to decomposition in these sites due to thaw.

2. Methods

2.1. Site description and experimental design

Study sites were located in the discontinuous permafrost zone (Brown *et al* 1997) of western Canada (59.5°N, 117.2°W), and included a burned peat plateau affected by wildfire in 2007, an intact peat plateau not burned at least in the last 70 years, and an adjacent thermokarst bog where we differentiate between a developmentally young thermokarst bog site near its edge and a mature thermokarst bog site in its center (figure 1). We selected sites with soil environmental conditions and peat stratigraphy that are representative of peat plateaus and thermokarst bogs in the region (Zoltai and Tarnocai 1975, Zoltai 1995, Pelletier *et al* 2017). Vegetation at the intact peat plateau consisted of a stunted, open-canopy black spruce (*Picea mariana* (MILL.) B. S. P.) forest with Labrador tea (*Rhododendron groenlandicum* OEDER) shrubs, and a ground cover of lichens (*Cladonia* spp.). At the burned peat plateau, fire had caused complete tree mortality, but vegetation recovery nine years after the fire was largely limited to Labrador tea and most of the ground was still charred. However, fire severity and peat combustion during this fire was likely low, as pre-fire lichen and litter could still be seen on the charred ground. Thermokarst bogs are associated with a drastic change of vegetation due to the associated water-logging and anoxic soil conditions when peat plateaus collapse (Camill 1999, Turetsky *et al* 2007). Accordingly, the thermokarst bog was treeless, and the young thermokarst bog was dominated by hydrophilic *Sphagnum riparium* ÅNGSTR. and water sedge (*Carex aquatilis* WAHLENB.) while the mature thermokarst bog was dominated by *Sphagnum fuscum* (SCHIMP.)

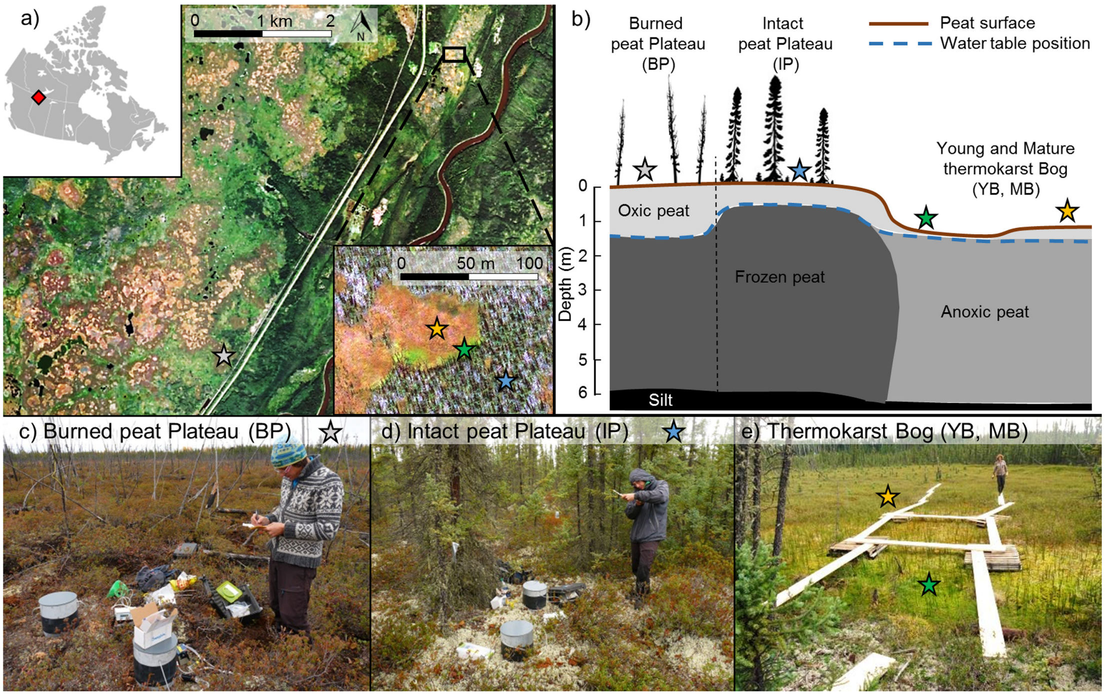

Figure 1. Study sites for monitoring respiration of aged soil carbon. (a) Study sites in northern Canada (59°N, 117°W). GeoEye satellite image obtained online https://zoom.earth. (b) Diagram indicating permafrost, oxic and anoxic conditions in the peat profiles of the sites. (c)–(e) Photos of sites: burned peat plateau, intact peat plateau, young thermokarst bog (front, collars installed within 0.5–2 m of the plateau edge) and mature thermokarst bog (back, collars installed within 10–15 m of the plateau edge). Photos of the intact and burned peat plateau each show a full-profile (open bottom) and near-surface (sealed bottom) collar pair enclosed by chambers.

KLINGGR. and leatherleaf (*Chamaedaphne calyculata* (L.) MOENCH) shrubs with scattered tussock cottongrass (*Eriophorum vaginatum* L.).

In 3rd–4th September 2016, we installed three pairs of PVC collars with 25 cm inner-diameter at the intact and burned peat plateau, and two pairs of collars each at the young and mature bog. In each pair, one collar was open at both ends and thus allowed for the entire peat profile to contribute to respiration as measured by chamber techniques (henceforth referred to as 'full-profile collar') while the other collar had a sealed bottom and thus excluded respiration from depths below the base of the collar ('near-surface collar') (Cooper *et al* 2017, Estop-Aragonés *et al* 2018). Installation of full-profile collars required inserting the collars in the soil to depths of 25 cm (intact and burned peat plateau) or 35 cm (young and mature thermokarst bog). Installation of the near-surface collars required extracting peat monoliths of 25 cm (intact and burned peat plateau) or 35 cm (young and mature thermokarst bog), inserting them into the near-surface collar, and reinserting the collar in the open pit. Stainless steel probes (6 mm outer-diameter, 1 mm wall thickness, Swagelok) were inserted near each collar pair to extract soil pore space CO_2 at depths of 50 cm (intact and burned peat plateau), 150 cm (young bog), and 200 cm (mature bog). These probes had a perforated base covered with a waterproof but gas-permeable membrane (Accurel GmbH, Wuppertal, Germany). Different depths of the probes were chosen to collect CO_2 from peat layers with similar age (approximately 1600 yrs BP, table S1 is available online at stacks.iop.org/ERL/13/085002/mmedia).

2.2. Peat profile characteristics and age determination

Soil cores were collected at the intact peat plateau, young and mature bog a year prior to collar installation. A Russian peat corer (4.5 cm inner-diameter, Eijkelkamp, Giesbeek, Netherlands) was used in thawed peat, and a Snow, Ice, Permafrost Research Establishment coring auger (10 cm inner-diameter) in frozen peat. We identified the transition from *Sphagnum* to sylvic peat at the young and mature bog, which indicates the shift from peat plateau to thermokarst bog vegetation and thus the timing of collapse (O'Donnell *et al* 2012). This transition depth was visually identified from the clear stratigraphic change between post-thaw and plateau peat (figure S1). Peat depths, as indicated by transition into underlying silt, varied between 500 and 600 cm among sites (peat depth at the burned site was determined to be >300 cm and was likely similar to the intact site). Peat samples from ten depths each from the intact peat plateau and mature bog cores were ^{14}C-dated (table S1) using accelerator mass spectroscopy (AMS) by separating 50–100 mg of clean, identifiable plant macrofossils analyzed in the A. E. Lalonde AMS Laboratory, Ottawa.

2.3. Measurements of CO_2 fluxes and $^{14}CO_2$

We measured CO_2 fluxes and collected CO_2 for ^{14}C analysis using dark chambers on 19th–21st September 2016. We chose to sample during fall because we consider the environmental conditions at that time of year favorable to detect the contribution of aged soil C to soil respiration. At time of sampling, vegetation was senescing and daytime air temperatures were <5 °C, while seasonal thaw depths and soil temperatures at 50 cm were near their annual maxima. Daily average soil temperatures at 50 cm were 1.5 °C, 6.6 °C, 9.2 °C and 9.5 °C at time of sampling at the intact plateau, burnt plateau, young bog and old bog, respectively, while maximum temperatures occurred in mid-August and were 2.7 °C, 9.5 °C, 14.1 °C and 12.1 °C (figure S2). Fluxes were measured by monitoring CO_2 concentration (EGM-4, PP Systems, Amesbury, MA, USA, accuracy ±20 ppm) inside deployed chambers (11 l) for 6 min. Linear regressions ($R^2 > 0.97$) of change in CO_2 concentration over time were used to calculate flux rates while accounting for differences in headspace volume and temperature. Fluxes from full-profile collars represent soil respiration (SR), and the difference between SR and fluxes from near-surface collars represents the respiration from sources deeper than the collar (SR_{Deep}). Note that SR_{Deep} is not a measure of the contribution of aged soil C to SR, due to potential respiration of young material translocated to deeper layers.

Collars were left enclosed after flux measurements until concentrations reached approximately 1500 ppm after which CO_2 was collected for ^{14}C analysis (Lupascu *et al* 2013): headspace air was circulated for 15 min (0.5 l min^{-1}) through drierite desiccant before passing through a molecular sieve (Zeolite 13X) to adsorb the CO_2. All connections were air-flushed before sampling. Sieves were also used to collect atmospheric CO_2 samples for ^{14}C analysis.

Deep pore space CO_2 was withdrawn from soil probes using evacuated gas canisters (0.5 l) and flow-restricting gas capillaries (0.010 × 0.063 × 30 cm, Fisher Scientific, Pittsburgh, PA, USA). Potential contamination from atmospheric CO_2 in the probe samples was prevented by evacuating the internal probe headspace and refilling with N_2 gas before connecting the canisters.

Soil temperatures down to 60 cm depth were measured using thermometer probes (Thermoworks, American Fork, UT, USA) near each collar at time of $^{14}CO_2$ sampling. We also determined that collar installation caused no significant effects on soil environmental conditions by measuring just after the $^{14}CO_2$ sampling soil temperature at 20 cm and surface soil moisture in the upper 6 cm (ML3 ThetaKit, Delta-T Devices, Cambridge, UK) in both type of collars (figure S3). Temperature loggers (HOBO Pendant, Onset, Bourne, MA, USA, accuracy ±0.53 °C) were installed one year earlier at the young and mature bog at 1, 2 and 3 m depth. Active layer depth at the intact and burned peat plateau was measured with frost probes.

The molecular sieves and gas canisters were sent to University of California, Irvine, for ^{14}C analysis (table S2). Carbon dioxide was released from sieves by baking at 630 °C for 45 min, or extracted from canisters using a vacuum line, purified cryogenically, and reduced to graphite via Zn reduction (Xu *et al* 2007). The ^{14}C content of the graphite was measured at UCI's W. M. Keck C Cycle AMS laboratory (NEC 0.5MV 1.5SDH-2) (Beverly *et al* 2010). The measurement uncertainty for ^{14}C was <0.002 fraction modern (fM). Values for ^{14}C are reported in fM notation and ages refer to conventional radiocarbon ages (uncalibrated) expressed as years before present (yrs BP). Fraction modern expresses the isotope ratio $^{14}C/^{12}C$ of the sample normalized to a ^{13}C of −25‰ to remove fractionation effects and divided by 0.95 the measured ratio of the OX-I standard (Stuiver and Polach 1977). By convention, this standard represents the pre-industrial atmospheric $^{14}CO_2$ in 1950 with fM = 1, and year 0 BP (before present) refers to AD1950. Atmospheric $^{14}CO_2$ peaked and nearly doubled (fM ~ 2) during early 1960s due to nuclear weapon testing and has been declining since as it becomes incorporated, mixed and cycled in the atmosphere, oceans and biosphere (Hua *et al* 2013).

2.4. Estimating contributions of aged soil carbon to soil respiration

The fM of respired CO_2 from each collar (fM_{Resp}) was calculated after accounting for the proportion of atmospheric and respired CO_2 (P_{Atm} and P_{Resp}) inside the chamber at the time of $^{14}CO_2$ sampling:

$$fM_{Resp} = \frac{fM_{Chamber} - P_{Atm} \times fM_{Atm}}{P_{Resp}}, \quad (1)$$

where $fM_{Chamber}$ and fM_{Atm} refers to the measured fM of CO_2 in the chamber and atmosphere, respectively. The sum of P_{Atm} and P_{Resp} is 1, and P_{Atm} is calculated from the measured CO_2 concentrations in the atmosphere ($[CO_2]_{Atm}$) and in the chamber ($[CO_2]_{Chamber}$) at the time of $^{14}CO_2$ sampling:

$$P_{Atm} = \frac{[CO_2]_{Atm}}{[CO_2]_{Chamber}}. \quad (2)$$

Carbon dioxide respired from aged soil C will have a lower fM value than that respired from recently photosynthetically-fixed C (table S1). Thus, CO_2 released from full-profile collars with a lower fM value than in near-surface collars indicates a contribution to SR from aged soil C. We estimated the fractional contribution of aged soil C to SR ($Contribution_{Aged}$) at each location using the fM value of CO_2 from the full-profile (fM_{RespFP}) and near-surface (fM_{RespNS}) collars and

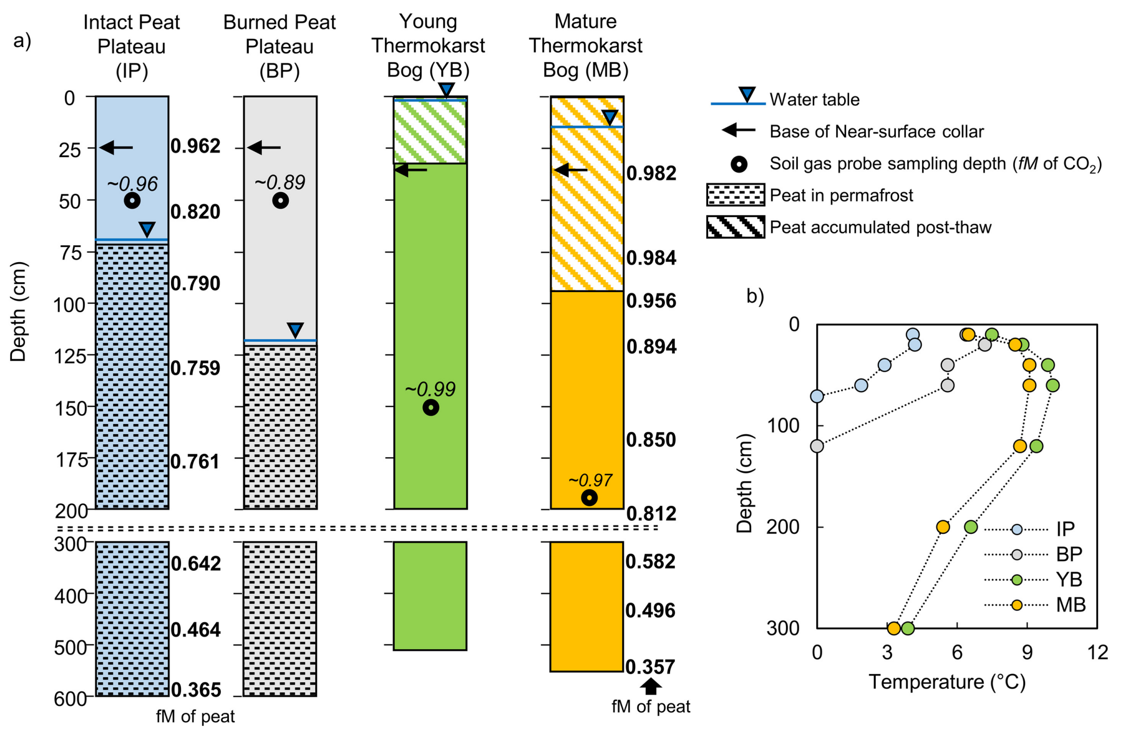

Figure 2. Physical and environmental characteristics of peat profiles at the study sites. (a) Peat profiles from each site with peat depth, active layer, water table, and peat type indicated. Fraction modern (fM) values of peat in the intact peat plateau and mature thermokarst bog sites are given next to each profile rounded to three decimals (see table S1 for ^{14}C analysis results). The values above the round symbol refer to the mean fM of the CO_2 collected at depth with the soil gas probes (50 cm in IP and BP, 150 cm in YB and 200 cm in MB), rounded to two decimals (table S2). Note the break and the different scale in the depth profile. The base of the near-surface collars is indicated with arrows at 25 cm (IP, BP) and 35 cm (YB, MB). The transition depth between post-thaw (*Sphagnum*) and sylvic peat occurred at 32 cm in YB and 88 cm in MB. (b) Soil temperature profiles at each site at date of $^{14}CO_2$ sampling (table S3).

the fM value of CO_2 from the probes which define the age of aged soil C ($fM_{AgedSoilC}$) (see supplementary information):

$$\mathrm{Contribution_{Aged}} = \frac{fM_{RespFP} - fM_{RespNS}}{fM_{AgedSoilC} - fM_{RespNS}}. \quad (3)$$

At two locations (one at the intact peat plateau and another at the young bog) there was insufficient CO_2 collected from the probes for ^{14}C determination, and we there used the mean of the available measurements within the same site to solve equation (3) (table S2). The estimate of $\mathrm{Contribution_{Aged}}$ depends on the ^{14}C signature of 'aged soil C' ($fM_{AgedSoilC}$) used in equation (3). Therefore, in addition of using the fM value of CO_2 collected with the probes to calculate estimates of $\mathrm{Contribution_{Aged}}$, we also performed a sensitivity analysis where we used fixed ages across all sites to yield alternative estimates. In the sensitivity analysis we assigned $fM_{AgedSoilC}$ a fixed value across all sites in equation (3), rather than the fM value of CO_2 sampled with the probes. These fixed values were based on the age of the peat at the depth of the probes as well as the age of the peat at >3 m. By multiplying $\mathrm{Contribution_{Aged}}$ with SR we estimated the rate of mineralization of aged soil C at each site (SR_{Aged}). The condition for a detection of $\mathrm{Contribution_{Aged}}$ is that fM_{RespFP} is lower than fM_{RespNS}. If fM_{RespFP} is greater than fM_{RespNS} the estimate of $\mathrm{Contribution_{Aged}}$ results in negative values, which we express as 0%.

2.5. Statistical analysis

All statistical analysis was carried out in R (Version 3.3.2) (R Core Team 2014). We performed t-tests to evaluate differences in fluxes and in $^{14}CO_2$ between collar types and one-way ANOVA to evaluate differences in fluxes between sites. When the ANOVA test indicated statistically significant differences between sites, we performed a post hoc Tukey HSD for pairwise comparisons of differences between sites. The suitability of parametric analysis was checked by examining the normal distribution and the homogeneity of variances of the data. For t-tests, the homogeneity of variances was checked using an F test. For ANOVA, the homogeneity of variances was checked using Levene's test in the car package (Fox and Weisberg 2011) in addition to Shapiro–Wilk test on the residuals to validate normality. Normality was also verified by visually inspecting the residuals with quantile-quantile plots. When the homogeneity of variances test failed, instead of a t-test, the non-parametric Wilcoxon test was used to check $^{14}CO_2$ differences between collar type in oxic soils (intact and burned peat plateaus). We define the statistical significance level at 5% or below in the text.

3. Results

3.1. Physical and environmental characteristics of peat profiles

All four sites had deep peat profiles, but physical and environmental characteristics differed significantly and determined the quantity and age of soil C available for decomposition at time of sampling (figure 2). Active layer depth at the intact peat plateau was on average 71 cm (60–80 cm range), with a peat age of about 1700 yrs BP (0.807 fM) at the active layer base (figure 2(a), table S1). Active layer depth at the burned site was on average 120 cm (88–141 cm range), which assuming a similar profile as at the intact site suggested a peat age at the active layer base of approximately 2100 yrs BP (0.767 fM). Peat depth at the intact peat plateau site was 6 m, with a basal date of about 8100 yrs BP (0.365 fM). Neither the intact nor burned peat plateau had a water table above the frost table. Soil temperatures at the burned site were 2.3°C–3.0 °C warmer than at the intact plateau at comparable depths throughout the active layer (figure 2(b)). Both the young and mature thermokarst bog had peat depths >5 m with a basal peat age of about 8200 yrs BP (0.361 fM) (figure 2(a), table S1). The transition between *Sphagnum* to sylvic peat was found at 88 cm depth in the mature bog, suggesting that thermokarst development occurred 360 yrs BP (0.956 fM) based on the peat ^{14}C measurements at the transition (figure 2(a), table S1). The transition from *Sphagnum* to sylvic peat was found at 32 cm depth at the young bog, suggesting that thermokarst development was more recent, likely within the last few decades based on ^{210}Pb dating in similar sites (figure S4). The water table was at the peat surface in the young bog, and 18 cm below the surface at the mature bog at the time of flux measurements. Soil temperatures were 0.3 °C–1.2 °C warmer at the young than the mature bog throughout the peat profile, but both thermokarst bog sites were up to 9 °C warmer than the peat plateau sites, particularly at depths >20 cm (figure 2(b)).

Our methodology for estimating the contribution of aged soil C to soil respiration (Contribution$_{Aged}$) requires that peat accumulated since the 1950s (i.e. peat with the ^{14}C bomb-peak) is fully contained within the near-surface collars. All near-surface collars at the plateaus and mature bog contained peat accumulated before the ^{14}C bomb-peak period (figure 2(a)). The bottom of near-surface collars corresponded to depths with peat ages of approximately 150 yrs BP (0.982 fM) at the mature thermokarst bog and 450 yrs BP (0.946 fM) at the intact peat plateau. We assume that the burned site has a similar peat profile as the intact peat plateau given their proximity and low fire severity. In the young bog the collars were installed to 35 cm depth and thus included 3 cm of sylvic peat below the *Sphagnum* peat (transition from *Sphagnum* to sylvic peat at 32 cm depth). Based on ^{210}Pb dating of similar young thermokarst bog cores from sites within the same region, we assume peat at the bottom of the near-surface collars (35 cm depth) accumulated before the ^{14}C bomb-peak period (figure S4). Given the slow accumulation of sylvic peat (Pelletier *et al* 2017, Estop-Aragonés *et al* 2018), this is likely a conservative assumption, and thus we consider the ^{14}C bomb-peak fully contained in the near-surface collars also at the young thermokarst bog site.

3.2. CO_2 flux measurements and $^{14}CO_2$ monitoring

Soil respiration (SR, i.e. CO_2 flux from full-profile collars) decreased in the order intact peat plateau > burned peat plateau > young bog > mature bog with statistically significant differences between the intact site and both young bog ($p = 0.034$, post hoc Tukey HSD tests) and mature bog ($p = 0.007$, post hoc Tukey HSD tests), and between the burned site and mature bog ($p = 0.039$, post hoc Tukey HSD tests) (figure 3(a)). A contribution to SR originating from sources at depths below the base of near-surface collars (SR$_{Deep}$) was found at all locations, as CO_2 fluxes from full-profile collars were consistently greater than fluxes from near-surface collars (figure 3(a)). SR$_{Deep}$ decreased in the order burned peat plateau > young bog > intact peat plateau > mature bog, but without statistically significant differences between sites ($p = 0.083$, one-way ANOVA test). The average relative contribution from SR$_{Deep}$ to SR decreased in the order young bog (49 ± 6%, ±1σ SD) > burned plateau (48 ± 13%) > mature bog (31 ± 17%) > intact plateau (21 ± 8%) (figure 3(a)).

A significant contribution of aged soil C to SR (Contribution$_{Aged}$), as suggested by SR$_{Deep}$, requires the fM values of CO_2 respired from full-profile collars to be lower than that from near-surface collars. Accordingly, we did observe a lower fM of CO_2 from full-profile than near-surface collars at all six peat plateau locations (3 pairs of collars each at intact and burned peat plateaus), but only at one of four locations in the young and mature thermokarst bog (figure 3(b)). As such, the CO_2 released from full-profile collars had significantly lower fM than that from near-surface collars ($p = 0.026$, Wilcoxon test) in sites with oxic active layers (intact and burned peat plateaus). In contrast, there was no significant difference in fM of CO_2 released between full-profile and near-surface collars ($p = 0.130$, two-sample independent t-test) in sites with predominately anoxic peat profiles (young and mature thermokarst bogs).

To estimate Contribution$_{Aged}$ using equation (3), we needed to define the age of 'aged soil C' (fM$_{AgedSoilC}$). Our first estimate of Contribution$_{Aged}$ defined aged soil C using the fM of CO_2 collected with probes at each location. The CO_2 from the probes had ages ranging from 180 to 540 yrs BP at the intact site, 440–1175 yrs BP at the burned, 95 yrs BP at the young bog, and 210–270 yrs BP at the mature bog (figure 3(b)). As such, the CO_2 collected by probes was

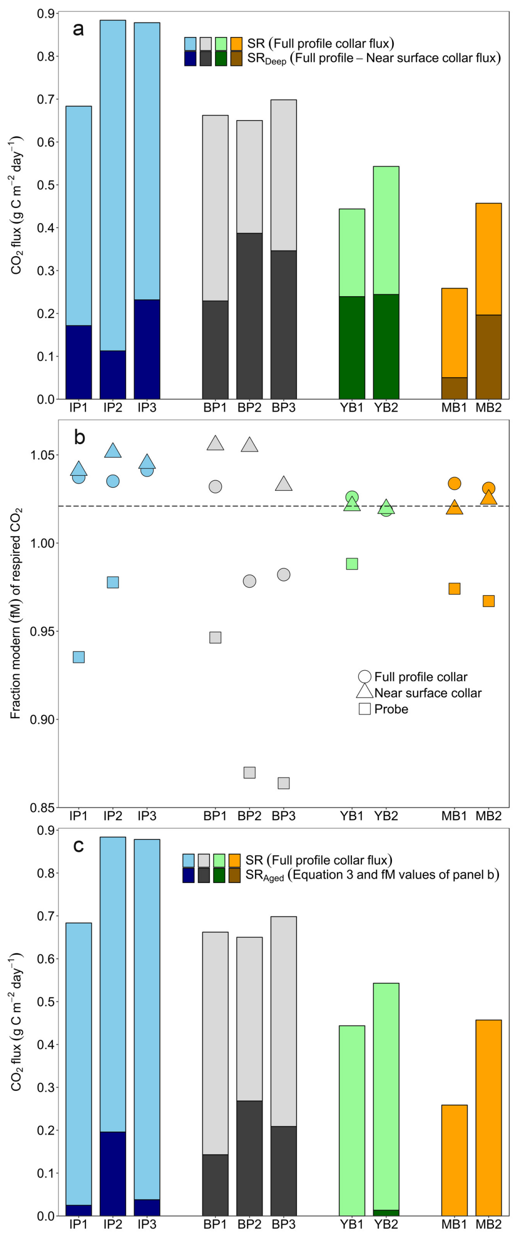

Figure 3. Soil respiration rates and ^{14}C content of CO_2 respired from locations in the intact (IP) and burned (BP) peat plateaus, and young (YB) and mature (MB) thermokarst bogs. (a) Soil respiration (SR), measured as CO_2 flux from full-profile collars, and the contribution to SR from deep sources (SR_{Deep}), calculated as the difference in CO_2 flux between full-profile and near-surface collars (n = 2–3 chamber pairs per site). (b) Fraction modern (fM) of respired CO_2 from full-profile and near-surface collars corrected for atmospheric CO_2, and of CO_2 collected from depth with probes (n = 2–3 chamber pairs per site, n = 1–3 probes per site). The dashed line indicates fM of ambient atmospheric CO_2 (fM_{Atm} = 1.021, n = 2). See table S2 for detailed $^{14}CO_2$ analysis results. (c) Soil respiration (SR) and contribution to SR from aged soil C (SR_{Aged}), estimated using equation (3) and fM values shown in panel (b).

1000–1400 yrs BP younger than the peat at the same depths as the probes (figure 2, tables S1 and S2). Using equation (3), $Contribution_{Aged}$ was estimated to be greater at the burned (30.9 ± 9.9%, ±SD) than the intact peat plateau (10.0 ± 10.5%), the difference being marginally significant (p = 0.066, two-sample independent t-test). Expressing this as a rate, SR_{Aged} doubled at the burned compared to the intact peat plateau (0.21 ± 0.06 and 0.09 ± 0.10 g CO_2–C m^{-2} d^{-1}, respectively) (figure 3(c)). Aged soil C contribution was only detectable at one of the four thermokarst bog locations (YB2; 2.5%) (figure 3(b)), representing a SR_{Aged} of 0.01 g CO_2–C m^{-2} d^{-1} (figure 3(c)).

Our sensitivity analysis indicates that differences in $Contribution_{Aged}$ and SR_{Aged} between sites were robust regardless of the assumption of aged soil C ($fM_{AgedSoilC}$) used (figure 4). For this sensitivity analysis we varied the definition of aged soil C between 1600 yrs BP (age of peat at depth of probes) and 4000 yrs BP (age of peat in a potential active layer deepening of >3 m). The contribution remains negligible on average at the young and mature thermokarst bog regardless of the definition of aged soil C, due to higher fM of CO_2 in full-profile relative to near-surface collars, which yields negative estimates. At the peat plateau sites, changing aged soil C to the age of the peat at the depth of the probes (1600 yrs BP) reduced $Contribution_{Aged}$ to 22.1 ± 11.3% in the burned and 3.5 ± 3.1% in the intact site with SR_{Aged} 0.15 ± 0.07 and 0.03 ± 0.03 g CO_2–C m^{-2} d^{-1}, respectively. Assumptions of yet older soil C led to lower estimates; assuming aged soil C of 4000 yrs BP reduced $Contribution_{Aged}$ to 11.4 ± 5.9% in the burned and 1.8 ± 1.6% in the intact peat plateau, and SR_{Aged} to 0.08 ± 0.04 and 0.02 ± 0.01 g CO_2–C m^{-2} d^{-1}, respectively (figure 4).

4. Discussion

Our findings suggest that soil aeration, rather than the quantity of soil C exposed to decomposition through thaw, was the main control on aged soil C respiration in fall at our sites. We could only detect a significant contribution from aged soil C to respiration at the peat plateaus, where the active layer was predominately oxic. Furthermore, the peat plateau that burned 10 years prior to the study was estimated to have a three to fivefold greater rate of aged soil C respiration than the intact peat plateau, and was associated with both warmer soils and deeper active layer (70 versus 120 cm on average). In contrast, respiration of aged soil C was minimal or undetected in the thermokarst bog regardless of whether thaw had occurred decades or centuries ago. Loss of aged soil C as CO_2 from the thermokarst bog was undetected despite its substantially warmer peat profile, and its much larger (>5 m peat) and overall older (~8000 yrs BP basal age) C store that was available for microbial activity.

The minimal mineralization of aged soil C (SR_{Aged}) in thermokarst bogs despite substantial respiration originating below the near-surface collars (SR_{Deep}) suggests that recent C sources largely dominated C cycling at depth. Recently photosynthesized carbon at the surface of bogs has been shown to be

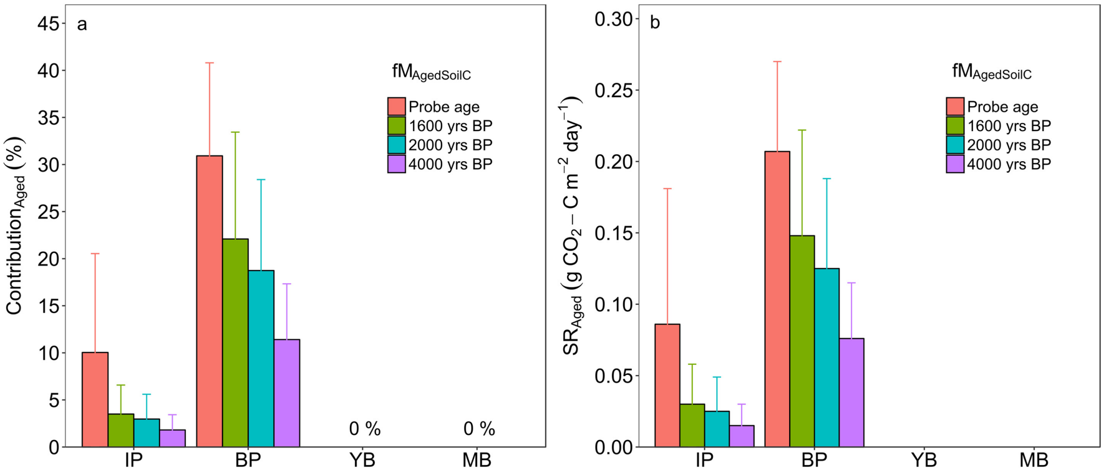

Figure 4. Estimates of (a) Contribution$_{Aged}$ and (b) SR_{Aged} in the intact (IP) and burned (BP) peat plateaus, and young (YB) and mature (MB) thermokarst bogs using different assumptions of the age of aged soil C ($fM_{AgedSoilC}$) in equation (3). This sensitivity analysis used the age of CO_2 from the probes at each location (probe age, varied between 95 and 540 yrs BP among sites—see text for details), or fixed ages of aged soil carbon (1600 yrs BP, 2000 yrs BP, and 4000 yrs BP) across all sites. The fixed ages of 1600 yrs BP and 2000 yrs BP were chosen considering the observed thaw depths at the peat plateau sites and the age of peat based on the ^{14}C data of the peat profiles (table S1). The fixed age of 4000 yrs BP represents an extreme scenario with a potential active layer deepening >3 m (the deepest active layer we measured was <1.5 m). Error bars show 1σ standard deviation ($n = 3$). Estimates for Contribution$_{Aged}$ at the thermokarst bog were negligible on average and only detectable in one young bog location (YB2), ranging between 2.5% (probe age) and 0.2% (4000 yrs BP).

leached several meters downward where it is available for mineralization, resulting in depth profiles of dissolved organic C (DOC), CH_4, and CO_2 that are substantially younger than the peat (Aravena *et al* 1993, Charman *et al* 1994, Chanton *et al* 1995, Chasar *et al* 2000, Wilson *et al* 2016). In agreement with these observations, our measurements of CO_2 collected at depth with probes were consistently younger than peat at the same depth (figure 2). Our CO_2 flux measurements indicated considerable respiration occurring at depths below the near-surface collar base with SR_{Deep} (i.e. full-profile collar minus near-surface CO_2 flux, figure 3(a)) being 20%–50% of the total flux across all sites. However, the estimates of SR_{Aged} were much lower (i.e. solved using equation (3), figure 3(c)). The discrepancy between SR_{Deep} and SR_{Aged} occurred in all sites but was more pronounced in the thermokarst bog. It is well established that thermokarst bog development causes rapid accumulation of peat at the surface (Camill 1999, Turetsky *et al* 2000, Jones *et al* 2017, Wilson *et al* 2017). The large difference between SR_{Deep} and SR_{Aged} could thus be explained by the translocation and mineralization at depth of leachates/exudates with recently fixed C from the productive *Sphagnum* mosses and sedges. The contribution of these recent C sources, in addition to spatial variability, could also explain observations of CO_2 with lower fM in near-surface than in full-profile collars in some sampling locations (YB1, MB1, MB2, figure 3(b)). In any case, the fact that respiration of aged soil C was so limited despite the very large C store available for decomposition is actually quite remarkable. The low or undetectable SR_{Aged} in the thermokarst bog could also be explained by the argued inactivation of anaerobic respiration due to energetic constraints when large pools of metabolic products accumulate in water-logged conditions (Blodau *et al* 2011).

Analysis of C stocks in Alaskan thermokarst bog cores suggest rapid loss of aged soil C within decades following thaw (Jones *et al* 2017) but we currently lack evidence for the processes explaining such large C losses following thermokarst development. Our findings in the late growing season in a deep peat deposit provide evidence against rapid old C losses as CO_2 during the thermokarst bog stage, but we cannot rule out substantial C losses either through CH_4, DOC, or as CO_2 at other times of the year or at sites with different permafrost/peatland development histories. The available measurements of $^{14}CO_2$ and $^{14}CH_4$ during the growing season in other thermokarst bogs (Klapstein *et al* 2014, Cooper *et al* 2017, Estop-Aragonés *et al* 2018) suggest low respiration rates of aged soil C that cannot explain the substantial reduction of C stocks in peat plateaus suggested by the analysis of soil cores in chronosequences (Jones *et al* 2017). Peat plateau edges may exhibit increased active layer depths extending 3–15 m onto the peat plateau (Baltzer *et al* 2014). Losses of aged soil C could occur in these near-edge areas during the decades just before thermokarst development if the soil profile remains oxic when the active layer deepens. Such losses could also occur through waterborne export of dissolved and particulate carbon but these measurements are not reported in permafrost peatlands and measurements in non-permafrost peatlands show considerably younger DOC than the peat (Chasar *et al* 2000, Campeau *et al* 2017). It also remains unknown if aged soil C losses occur during winter when the pool of translocated young DOC at depth may become exhausted. Additionally, differences regarding peat incorporation in permafrost could influence its susceptibility to mineralization post-thaw; the bulk of the peat in our sites accumulated under non-permafrost stages whereas it was rapidly incorporated in permafrost in the Alaskan sites (syngenetic permafrost). Overall, the dearth of available data cannot explain the inferred large C losses following thermokarst development (Jones *et al* 2016) and further measurements are needed to characterize the spatial and temporal variability of aged soil C mineralization following thaw in peatlands.

This study shows that wildfire has the potential to both increase and decrease respiration of aged soil C through deepened active layer and accelerated thermokarst, which suggests that the overall influence will be dependent on temporal trajectories of soil thermal recovery and thermokarst expansion following wildfire. We observed increased release of aged soil C with active layer deepening when comparing the intact and burned plateaus but not in our thermokarst bog. Wildfire causes a deepening of the active layer, an effect which lasts about 20 years before recovery of the soil thermal regime is complete and active layer depth returns to values before disturbance (Gibson *et al* 2018). However, wildfire also accelerates thermokarst bog development (Zoltai 1993, Myers-Smith *et al* 2007). Several factors such as the intensity of disturbance, local climate and landscape position (Jorgenson *et al* 2010) likely influence the thaw trajectory towards either recovery or thermokarst development. Critically, the time elapsed between a fire event and the potential thermokarst development would determine the exposition of aged soil C to oxic conditions in a deepened active layer stage before transitioning into anoxic conditions in thermokarst bogs. Thus, the peatland thaw trajectory would largely control the exposition time to either oxic or anoxic soil conditions potentially determining the magnitude of permafrost (aged) C loss. The intensified fire regime over the last 30 years (Gillett *et al* 2004, Kasischke *et al* 2010), with about 25% of peat plateaus burned in western Canada, further emphasizes the need to consider differences in thaw trajectories following wildfire to project future peatland C storage.

5. Conclusions

We present estimates of *in situ* mineralization rates of aged soil C released as CO_2 at the end of the growing season in permafrost peatlands with contrasting soil environmental conditions. Sampling locations dominated by soil oxic conditions in peat plateaus resulted in detectable contributions of aged soil C loss, and rates of aged soil C loss were about five times greater in the fire-affected site associated with a deeper and warmer active layer than in the intact peat plateau. In contrast, contributions of aged soil C were low or undetected in the water-logged and anoxic soils at the thermokarst bog both in locations thawed decades and centuries ago. If these observations are representative of processes occurring throughout the year, our results have important implications for our understanding not only of the response to thaw of aged peat carbon stocks but also of belowground carbon cycling in northern peatlands.

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